

THE GENUS *PORPHYRA* ON SOUTH AFRICAN COASTS:

I. OBSERVATIONS ON THE AUTECOLOGY OF *PORPHYRA* *CAPENSIS* SENSU ISAAC (1957), INCLUDING A DESCRIPTION OF DWARF PLANTS.

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ABSTRACT

The various forms of *Porphyra capensis* are described and discussed from the points of view of external morphology, vegetative cell structure and arrangement of reproductive bodies. Developmental changes are shown to occur in vegetative cell structure. It is possible that the pattern of development is influenced by environmental factors. Both dioecious and monoecious plants occur, but variations in spore arrangement are not consistently related to any other morphological or anatomical features. There is no definite evidence of sexuality in carpospore formation.

The occurrence of dwarf plants, reproducing by means of monospores, is recorded and their possible relation to normal-sized plants of *P. capensis* is discussed.

INTRODUCTION

The autecology and life history of several species of *Porphyra* have received attention over a number of years (Drew 1954, Tseng and Chang 1955, Graves 1955, Krishnamurthy 1959, Miura 1961, Conway 1964) and it is perhaps surprising that no consistent pattern of biology applicable to the genus as a whole has yet emerged. The occurrence of a microscopic filamentous phase, the *conchocelis*-phase, is well known. There have also been reports of "dwarf plants" (Tseng and Chang 1955) or "plantlets" (Drew 1954, Conway 1964, 1966) usually described as having the same form as the familiar leafy parenchymatous thallus but considerably smaller and reproducing by means of monospores only. The significance of these phases as regards the life cycle of *Porphyra* remains obscure, however, partly because of a lack of agreement in the accounts as to the method of formation and fate of the reproductive bodies produced by the full-sized parenchymatous plant.

While the present paper does not attempt to solve these basic problems, it is hoped that it will be of value in presenting a more complete picture of the biology of *Porphyra capensis* than is at present available. For the purpose of this paper the name *P. capensis* is used in the sense in which it is used by Isaac (1957). Further reference to the taxonomic position is made in the discussion.

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OBSERVATIONS ON FULL-SIZED PLANTS

1. Range of form.

The recorded distribution of *Porphyra capensis* is shown in Fig. 1. For details of its distribution the reader is referred to the account by Isaac (1957), but it is sufficient here to say that maximum development, in terms of both number of plants and size of individuals, occurs in the relatively cold waters of the west coast and that there is a general decline in luxuriance as one passes from west to east.

As Isaac points out, three main growth forms are found. The commonest form on the west coast has a large cordate to reniform thallus, dark olive-green or dull purple in colour and cartilaginous in texture (Plate I (a)). Plants of this kind are characteristically perennial, growing between about mid-tide level and high water level of neap tides, although isolated plants may be found down to the sublittoral fringe. These low level plants are usually epiphytic, often on *Aeodes orbitosa* and occasionally on the kelp *Ecklonia maxima*. In exposed situations, where wave action results in some splash, considerable numbers of plants may grow above the normal upper limit. These plants are always smaller and paler in colour than those at lower levels (Plate I (b)). High level individuals do not survive for any length of time but are replaced repeatedly by crops of young plants which are usually brown in colour and very variable in form (Plate II (a)).



FIG. 1.

Map showing the recorded distribution range (cross-hatched) of *Porphyra capensis*. Localities for dwarf plants are ringed.

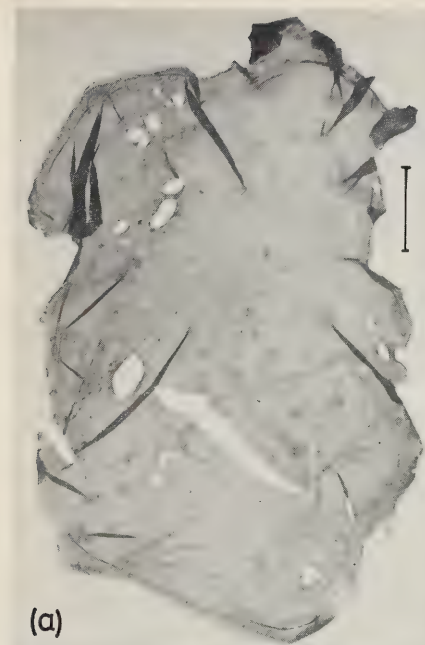


PLATE I.

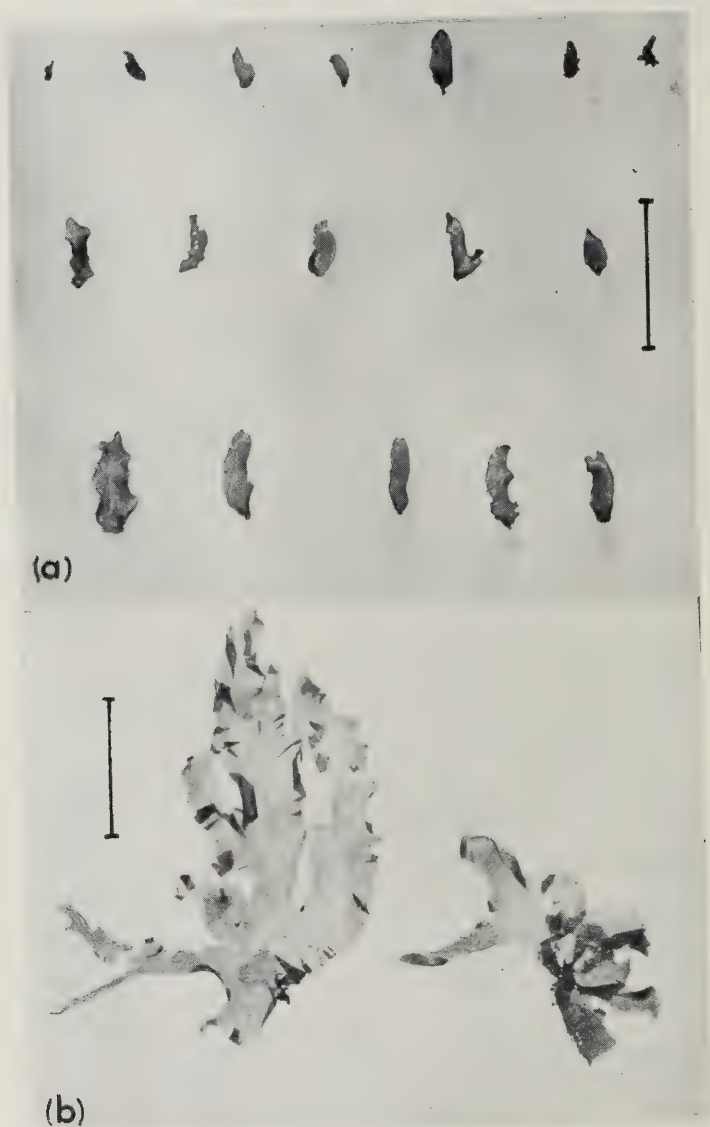


PLATE II.

The second form is characteristic of the relatively warm waters of False Bay and of the south and east coasts. It is basically similar to the high level type described above, although the thallus texture of the warm water form is usually more delicate. Due probably to the fact that the thin thallus is easily torn, these plants are often deeply laciniate (Plate II (b)).

The third form is found in sheltered situations. In the absence of much wave action young plants tend to elongate rapidly, the thallus broadening only slightly as it matures, so that it eventually acquires a linear to lanceolate form (Plate I (c) and (d)). In certain localities on the west coast large numbers of these elongated, ribbon-like plants occur. Many are ephemeral, developing rapidly during the winter or spring and dying off again in the summer months, although they do not necessarily appear as regular annuals.

2. Vegetative structure.

The thallus is always monostromatic. In very young plants of all forms the cells as seen in transverse section of the thallus are oval to rectangular, slightly longer than broad, each with a single, axile, stellate chromatophore which is usually brownish red in colour and has a prominent central pyrenoid (Fig. 2.A.). As growth proceeds the cells tend to elongate in a plane at right angles to the surface, the total thickness of the thallus increasing correspondingly. The chromatophore also becomes stretched longitudinally.

It appears that under optimal conditions of growth the elongation of the cells is very marked, takes place rapidly and is accompanied at an early stage by division of the chromatophore so that each cell of the mature thallus has two chromatophores. In typical west coast plants the cells may already have two chromatophores by the time the young plant is 1 cm in length. At first the

PLATES I AND II.

Various growth forms of the normal-sized parenchymatous phase of *Porphyra capensis*. Scale line represents 5 cm. in all cases.

PLATE I.

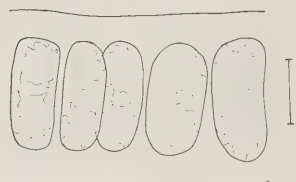
- (a) Cartilaginous reniform "male" plant. Bakoven, west coast of Cape Peninsula, February 1967.
- (b) Typical plants from high water of neap tides level. Granger Bay, Cape Town. March 1967.
- (c) "Male" (left) and carposporic plants of the linear, dioecious form. Llandudno, west coast of Cape Peninsula. September 1966.
- (d) Monoecious plant. Carposporic areas are visible as dark patches on the paler background of the spermatial areas. Melkbosch Strand, 12 miles north of Cape Town. March 1967.

PLATE II.

- (a) Young plants. Melkbosch Strand, March 1967.
- (b) "Male" (the smaller) and carposporic plants of the delicate, laciniate form. St. James, False Bay, May 1952.



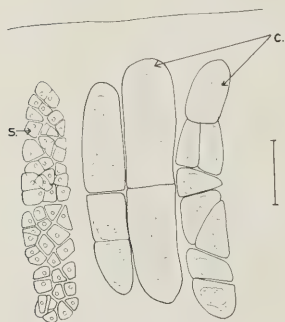
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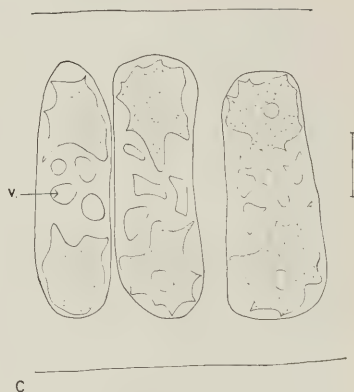
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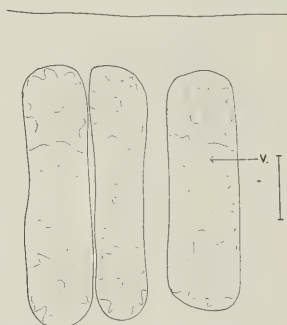
D.



F.



C.



E.



G.

two chromatophores retain the marked stellate form characteristic of the very young plant and are close together, so that they practically fill the protoplast of the cell. Vegetative cells frequently have this appearance in plants just starting to produce spores (Fig. 2.B.). As elongation of the cells continues, the chromatophores move one to each end of the cell. Numerous vacuoles are usually present in the central area of colourless cytoplasm. The chromatophores eventually lose the narrow extensions which give them a stellate form in the young cells and become lobed. Their colour also changes from brown to dark green and the pyrenoids become less distinct (Fig. 2.C. and E.). The total thickness of the thallus of the mature plant is very variable but is usually between 90 and 125 μ . At this stage the thallus has acquired its characteristic cartilaginous texture.

A few plants having the mature structure just described may be found in regions of relatively warm water, for example in False Bay. However, the delicate texture typical of the vast majority of warm water plants is associated with the fact that the cells retain the juvenile form. In these the vegetative cells elongate only slightly, most retaining the single chromatophore and the total thickness of the mature thallus does not usually exceed 65 μ (Fig. 2.D).

3. Reproduction and spore types.

In common with other species of *Porphyra*, *P. capensis* produces large numbers of two distinct types of spore. These are the deeply pigmented bodies commonly known as carpospores and the much smaller, colourless spermatia. In addition relatively small numbers of a third type of spore-like body may be released from certain thalli. For convenience these may be termed accessory spores.

FIG. 2.

A. T/S living thallus of a very young plant of *P. capensis* showing single stellate chromatophore with central pyrenoid in each cell. Material from Three Anchor Bay, Cape Town. March 1967.

B. C. D. and E. T/S living thalli of four mature (i.e. fertile) plants of *P. capensis* showing vegetative cells, v = vacuoles.

B. Lanceolate form from Bakoven, west coast of Cape Peninsula. February 1967.

C. Lanceolate form from Melkbosch Strand, approximately 12 miles north of Cape Town. March 1967.

D. Delicate, lacinate form from St. James, False Bay. April, 1967.

E. Reniform plant from Bakoven. February, 1967.

F. T/S fertile thallus margin of monoecious plant of the "sector" type, the section taken across the dividing line between spermatial and carposporic sectors. s = spermatium. c = dividing carpospore mother cells. Melkbosch Strand. March, 1967.

G. T/S fertile thallus of carposporic plant, showing remains of trichogyne-like extensions of the mother cells and corresponding humps of surface matrix. Kommetjie, west coast of Cape Peninsula, April, 1955. Scale line represents 20 μ in all cases.

The original accounts of the species (Kützing 1849, Agardh 1883) do not distinguish the various spore types nor do they indicate whether the plants are monoecious or dioecious. *P. capensis* has generally been regarded, however, as typically dioecious, or, if monoecious, then of a rather peculiar type in which the carpospores and spermatia are produced in different sectors of the thallus, separated by a sharp line of demarcation (Isaac 1957, Fig. 2). For the majority of plants throughout the geographical range this description is accurate. Carposporic plants (or sectors of plants) are characterised by a deep red or pink margin, while those producing spermatia have a yellow or cream margin (Plate I (c)). The paler colour in each case is associated with a thinner thallus. The ephemeral linear or lanceolate form is very prolific in spore production and this has a marked effect on the colour of the mature thallus, particularly in the case of the carposporic plants, in which almost the entire thallus becomes deep red.

On the west coast some monoecious individuals occur, particularly at low levels, in which packets of carpospores and spermatia are borne in irregular intermingled patches. Such plants are usually ephemeral, roughly 10% of the individuals in populations of the linear to lanceolate form being of this type. In terms of morphology and vegetative structure they are indistinguishable from dioecious plants (Plate I (d)). Monoecious plants of this type have not so far been found in False Bay or further east.

The terms "carpospore" and "spermatium" are used here for convenience only, since there is no convincing evidence that any sexual process is involved in reproduction in *P. capensis*. This is in keeping with the findings of workers who have investigated northern European species (Krishnamurthy 1959, Conway 1964). Occasionally carposporic plants are found in which the cells near the thallus margin have elongated extensions of the protoplast at one or both ends, similar in appearance to the trichogynes which have been figured for *P. tenera* (Kunieda in Fritsch 1945, vol. II, p. 432, fig. 144 J; Tseng and Chang 1955a). These extensions may be very pronounced, the surface matrix being raised above them in a series of humps (Fig. 2.G). However, this phenomenon is by no means common and furthermore no spermatia have been found in any way associated with the trichogyne-like structures.

No change in the thickness of the thallus accompanies spore formation. Typical cold water plants, in which the vegetative cells are elongated and have two chromatophores, develop correspondingly elongated spore packets, approximately 128 spermatia or 32 carpospores being formed per mother cell. The form of the spore packets and approximate number of spores is the same whether the plant is dioecious or monoecious of either type. The first division of the mother cell is usually transverse in the formation of both carpospores and spermatia (Fig. 2.F). Mature carpospores in general lie in 8 tiers of 4 spores each and mature spermatia in 16 tiers of 8 each. However, neither the number nor the

arrangement of the spores is constant and many of the divisions may be oblique (Figs. 2.G and 3.A).

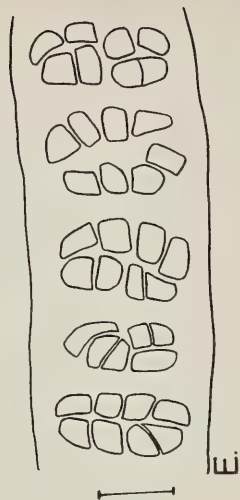
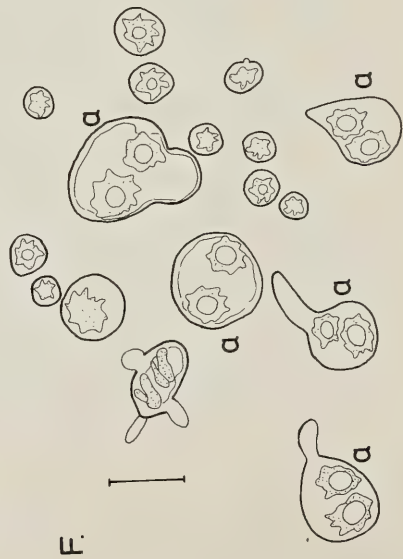
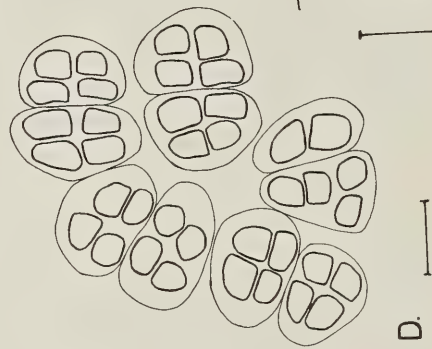
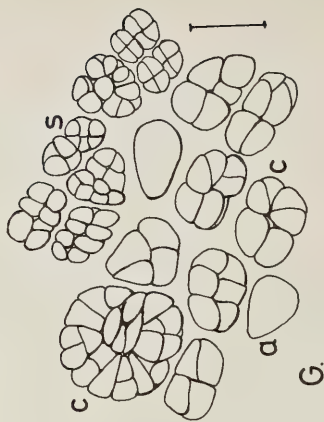
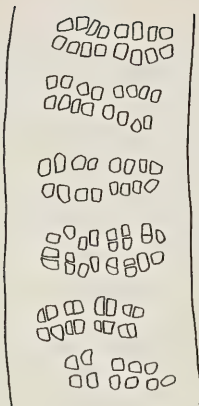
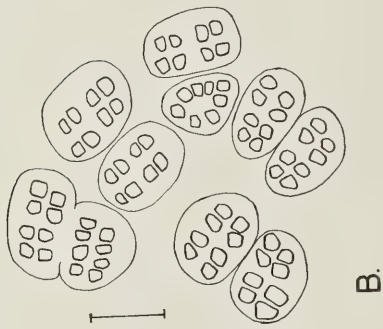
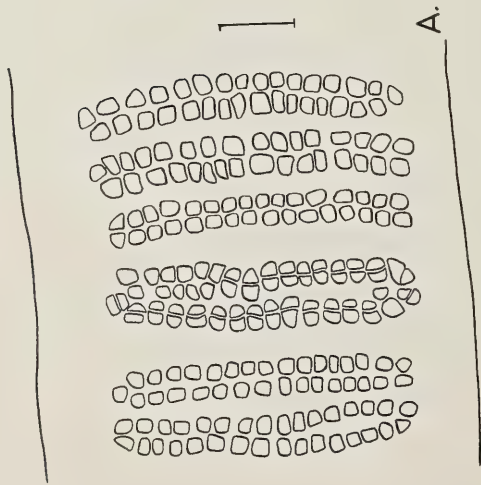
In plants in which the vegetative cells are only slightly elongated, the number of spores formed from each mother cell is approximately half the number typical of cold water plants; that is to say, 16 carpospores in 4 tiers of 4 spores each and 64 spermatia in 8 tiers of 8 spores each (Fig. 3.B, C, D and E).

In the case of the "male" thallus every cell in the fertile region divides to form spermatia. In some carposporic thalli (or the carposporic areas of monoecious plants) division of the cells in the fertile region appears to be in some way inhibited. Many cells fail to divide at all and remain greenish in colour while others divide irregularly so that the number of carpospores formed per mother cell is very variable (Fig. 3.G).

In such cases the first division of the mother cell is often longitudinal instead of transverse, one daughter cell remaining undivided while the other forms carpospores. If undivided cells are in the majority, the fertile margin of the plant appears pale greenish brown in colour with a number of red streaks indicating the presence of developing carpospores. The appearance is very similar to that figured by Smith (1944 plate 38, Fig. 2) for *P. lanceolata* (Setchell and Hus) G. M. Smith, and described by him (p. 170) as "packets of carpospores in hieroglyphic-like lines".

Undivided cells, including those daughter cells of potential carpospore mother cells which fail to divide further, may be released as spore-like bodies which may be termed accessory spores. The term "monospore" is not applicable since cell division may precede spore formation. Once released the accessory spores may be distinguished from carpospores by their greenish colour and larger size (20—35 μ), although the latter is not always a reliable guide since the carpospores are very variable in size. Accessory spores produced by typical cold water plants are often recognizable because of the presence of two chromatophores in each spore in contrast to the single one characteristic of the carpospore (Fig. 3.F). As yet attempts to induce accessory spores to germinate under culture conditions have been unsuccessful. In a few cases germ tubes have been formed as shown in Fig. 3.F, but growth has not proceeded further and it is not even possible to say whether sporelings are likely to be filamentous growths or parenchymatous thalli.

The carpospores without exception each have a single red or deep pink chromatophore. At the time of shedding there is a wide variation in size (10·0 μ —20·3 μ), even amongst spores shed by a single thallus. After they are released the spores enlarge considerably and numerous vacuoles appear in the cytoplasm. For some time before germination they undergo amoeboid changes of shape.



Germination takes place readily in culture and filamentous growths are formed which develop into a typical *conchocelis*-phase (Graves 1955; see also Plate IV) similar in all essentials to those which have been described for other species (Drew 1954, Tseng and Chang 1955).

THE DWARF PLANTS

1. Field Observations.

This account is based on the following collections examined: CAPE PROVINCE, East London, 17.ix.1955, *Graves P.59*. East London 18.vii.1965, *Graves P.60*. Port St. Johns (First Beach) 10.vii.1959, *Isaac*. Beach on the farm Brandfontein (approximately 10 miles west of Cape Agulhas) 8.xii.1964, *Graves*. NATAL. Salt Rock Beach (hotel rocks) 26.ix.1953, *Isaac*. These localities are also indicated in Fig. 1.

The plants in all three collections made by the author were growing at a level approximately midway between high water level of neap tides and low water level of neap tides, that is to say in a position typical for *Porphyra capensis*. No information as to level was available with the material collected by Isaac. However, the plants from Port St. Johns were attached to shells of the barnacle *Chthamalus dentatus* which indicates an upper midlittoral position.

At the Brandfontein farm locality large numbers of full-sized *P. capensis* plants were also present, growing in close proximity to the dwarf ones. At East London no full-sized plants were found on either occasion. The species is never common in this eastern part of its range (Isaac 1957). It will be noted that Port St. Johns represents the eastern limit of the recorded distribution of *P. capensis*, while the Salt Rock Beach locality is well beyond the range of full-sized *Porphyra* plants.

FIG. 3.

- A. T/S fertile thallus margin of "male" plant of *P. capensis* showing 16 tiers of spermatia in each spore packet. Kommetjie. April, 1955.
- B. Surface view and
- C. T/S of fertile thallus margin of "male" plant, showing packets of spermatia made up of 8 tiers of 8 spores each.
- D. Surface view and
- E. T/S of fertile thallus margin of carposporic plant, showing packets of carpospores made up of 4 tiers of 4 spores each. Both plants from Port St. Johns. January, 1939.
- F. and G. Spore types in *P. capensis*.
- F. Carpospores and germinating accessory spores (a) from a carposporic plant collected at Bakoven, June, 1965. Drawn from living material.
- G. Surface view of fertile thallus margin of monoecious plant showing spermatia (s), carpospore packets containing variable numbers of carpospores (c), and undivided cells (a). Llandudno, west coast of Cape Peninsula. December, 1966. Scale line represents 20 μ in all cases.

Dwarf plants are easily distinguishable in the field by their bright rose-red colour and, when fertile, by the delicate pink margin caused by the production of large numbers of monospores. Ordinary juvenile plants of *P. capensis*, as already stated, are brownish in colour and they never produce spores. Also the dwarf thalli are uniformly shaped (cordate to reniform) and tend to be crowded together in small isolated patches rather than distributed over a wide area.

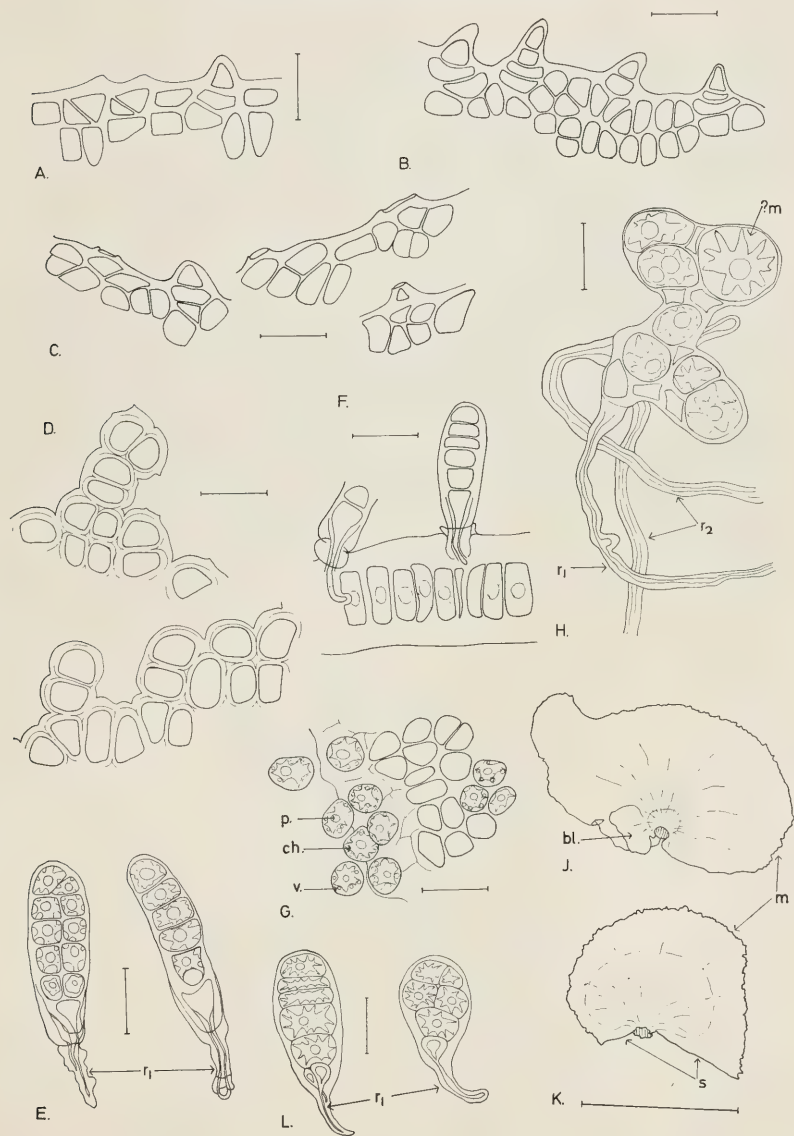
2. Morphology, structure and spore production.

The very young dwarf plants are identical in colour and form to the plants formed at the germination of the conchospore of the *conchocelis*-phase of *P. capensis* (cf. Fig. 4 E and L).

Up to six cells are formed at first in a uniseriate row, the basal cell distinct and producing a thick-walled, colourless, primary rhizoid. At this stage longitudinal divisions begin and become more frequent so that the thallus broadens first to a lanceolate and then to a cordate form. At this stage the thallus is from 1.0 to 2.0 mm long and about the same breadth at the broadest part. Secondary rhizoids from the basal cells form a small, disc-like holdfast. In section the cells are very similar to those of ordinary juvenile plants of *P. capensis* except that they are much smaller and the single, stellate chromatophore

FIG. 4.

- A, B and C. Serrated thallus margins of dwarf plants.
 A. Early stage in the development of serrations, showing oblique divisions of marginal cells. Port St. Johns material.
 B. Part of the serrated thallus margin of a sporulating dwarf plant. Brandfontein material.
 C. Thallus margin of a mature dwarf plant showing erosion of serrations. Graves P. 60 material.
 D. Parts of the fertile thallus margin of the plant shown in K, showing large, rounded potential monospores. Drawing made from preserved material in which there has been some shrinkage of the protoplasts.
 E. Two of many young plants found attached to dwarf plants at the Brandfontein farm locality, December, 1964. r_1 = primary rhizoids.
 F. T/S thallus of a dwarf plant passing through the bases of two epiphytic young plants like those shown in E. The primary rhizoids of the epiphytes may be seen penetrating the matrix and growing towards the "host" cells. Graves P. 60 material.
 Drawn from preserved material; protoplasts stippled.
 G. Part of the fertile thallus margin of a living dwarf plant showing release of monospores. Brandfontein material. ch = chromatophore. p = pyrenoid. v = vacuole.
 H. Young plant formed in culture as a result of germination of a monospore from a dwarf plant. Spores obtained from Brandfontein material. Culture 27 days old. r_1 = primary rhizoid. r_2 = secondary rhizoid. ? m = ? potential monospore.
 J. and K. Morphology of dwarf plants. Holdfasts are crossed-hatched.
 J. Plant from Graves P. 59 material, showing small secondary blade (bl.). Fertile region of thallus margin (m) not sharply demarcated from sterile region, which in this case is smooth.
 K. Plant from Salt Rock Beach material, showing abrupt demarcation between the fertile region of the thallus margin (m) and the sterile, serrated region (s).
 L. Young plants of the parenchymatous phase of *P. capensis* formed as a result of the germination of conchospores. Drawing made from living material taken from a 9 month old culture of the *conchocelis*-phase. r_1 = primary rhizoids. In J. and K. scale line represents $\frac{1}{8}$ in., in all others 20 μ .



in each cell is deep rose red in colour. The total thickness of the thallus is variable, but in general it is less than that of the ordinary juvenile plant. In the material examined the height of the cells varied between 13.7 and 21.2μ . The total thickness of the thallus was from 25.0 to 36.2μ .

In general the margins of the young plants become distinctly serrated (Fig. 4. B.). The development of a serration may be seen at first as an oblique division of one of the marginal cells, accompanied by a slight protuberance of the surface gelatinous matrix (Fig. 4. A.). The serrations are usually evenly distributed around the margin, but may be developed on one side of the thallus only.

As the thallus broadens the attachment becomes distinctly umbilicate in most cases. The blade remains entire and usually there is only one blade per holdfast, although the plants may be so crowded together that several appear to arise from a single base. Occasionally very small secondary blades do proliferate from the holdfast (Fig. 4. J.).

The mature thallus is in most cases broadly reniform but the shape may be considerably modified by spore production. This begins and is most vigorous along the upper edge furthest from the holdfast, but spreads gradually around the margins. There is usually an abrupt demarcation between the sterile serrated margin near the base of the plant and the upper fertile region (Fig. 4. K. and Plate III (a)). A small proportion of plants have smooth margins with no serrations at all. In these spore production appears to take place evenly around almost the entire margin so that the thallus has a rounded appearance as compared with thalli having serrated margins. All the plants of the Graves p. 59 collection were of this type and there were a few amongst the p. 60 material (Fig. 4. J. and Plate III (b)).

Even if a dwarf plant is not actively sporulating, the fertile margin is recognizable because of its very irregular appearance. The potential spores are larger and more rounded than the ordinary vegetative cells of the thallus and they protrude in irregular groups (Fig. 4. D.). In spore formation the entire contents of a marginal cell rounds off and is released as a single spore, no evidence of cell division immediately preceding spore formation having been found at all (Fig. 4. G.). It therefore seems reasonable to apply the term "monospore" to these structures. During spore production every cell in the fertile region produces a spore so that a large number of empty cell walls remain, visible to the naked eye as a pale pink or almost colourless margin to the thallus.

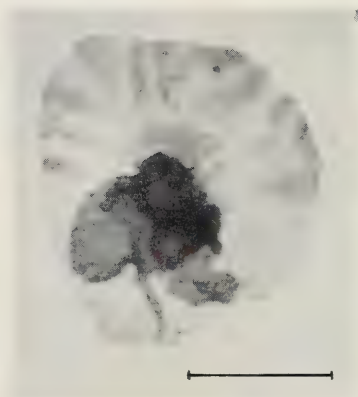
PLATE III.

Dwarf *Porphyras* from East London. July 1965 (Graves P. 60). Scale line represents 1 mm in both cases.

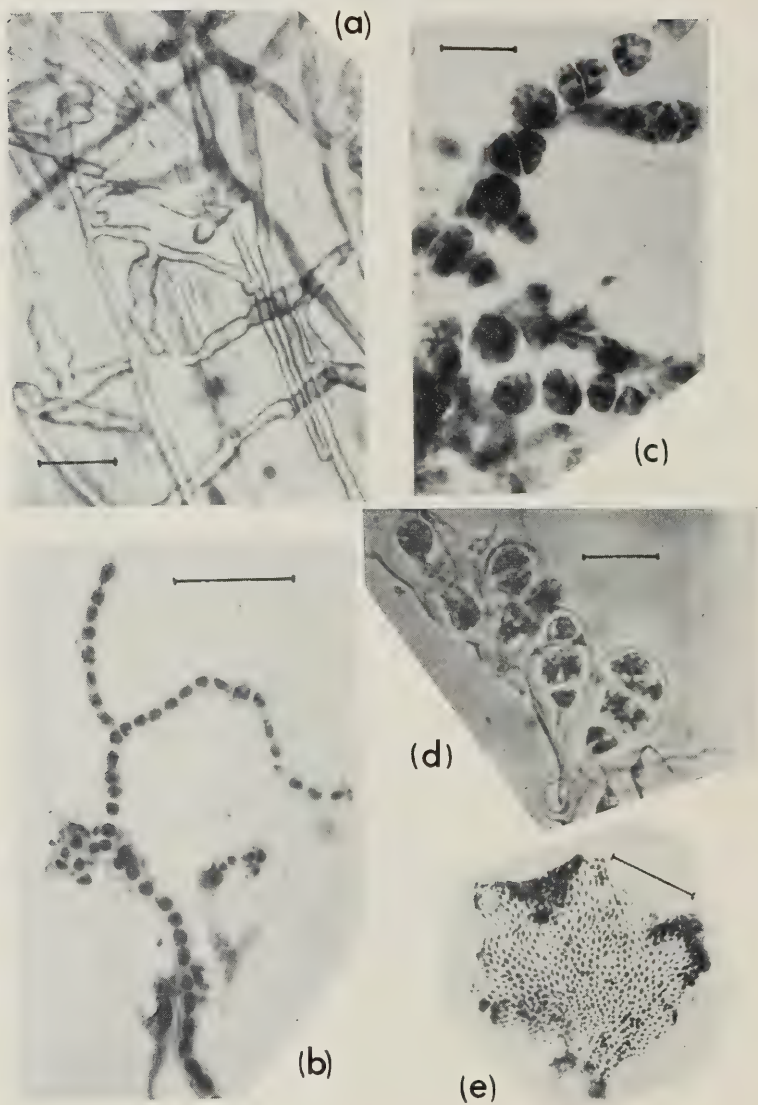
- (a) Reniform plant showing irregular fertile margin sharply demarcated from the sterile margin on either side of the prominent holdfast.
(b) Umbilicate, rounded plant sporulating around the entire margin.



(a)



(b)



Monospores are very similar in appearance to carpospores and conchospores and are of the same order of size, being from 10–14 μ in diameter. The single stellate chromatophore in each monospore is deeper in colour and has a more prominent pyrenoid than is the case with the other spore types, however. Numerous vacuoles are usually visible in the colourless cytoplasm surrounding the chromatophore and, like carpospores, monospores exhibit amoeboid changes of shape after their release.

Observations on the germination of monospores were made from the Brandfontein material. Some of the dwarf plants were placed in a petri dish of sterile sea water and the spores shed from them were collected on glass slides. After ten days large numbers of sporelings had developed. In all cases germination was bipolar. The primary rhizoids and later also the secondary ones were abnormally long and the young plants became very irregular in form as compared with those growing under natural conditions (Fig. 4. H.). In some of these thalli one or two of the cells were enlarged (? m in Fig. 4. H.) and similar in appearance to those illustrated as monospores by Conway (1964, plate II, fig. 11, p. 352) in her account of dwarf plantlets of *P. umbilicalis* (L.) J. Ag. In the material under discussion no release of spores was observed, however, and the form of the cells seemed to be merely an expression of the general difformity of the thalli. Similar abnormalities in growth had previously been observed in the development, in culture, of some conchospore sporelings.

In the field monospores are obviously produced in large numbers and germinate rapidly. Most of the mature plants collected at Brandfontein had large numbers of sporelings growing epiphytically on them. In section one could see that the rhizoids penetrated quite deeply into the gelatinous matrix of the "host" plant. They showed an apparent tendency to grow towards the "host" cells which in places had depressions in their protoplasts where the rhizoids had come into contact with them (Fig. 4. F.). There was, however, no definite indication of parasitism.

PLATE IV.

Conchocelis-phase of *P. capensis*. In (a), (c) and (d) the scale line represents 20 μ .

Others as indicated. With the exception of (a), all from a 9 month old culture.

- (a) Early stage in the development of the *conchocelis*-phase, showing fusions between adjacent threads embedded in an oyster shell flake. Culture 25 days old.
- (b) A long sporangial branch and some vegetative threads. Scale line represents 100 μ .
- (c) Mature sporangial branches in which the cross walls between the sporangia have mostly broken down to form sporangial tubes containing the conchospores. In some cases the contents of the sporangium have divided to form two spores.
- (d) Young plants of the parenchymatous phase formed from conchospores which have germinated while still enclosed within the sporangial tube.
- (e) A larger plant of the parenchymatous phase formed as a result of the germination of a conchospore. Scale line represents 0.25 mm.

In size fertile dwarf plants range from 2.0 to 4.0 mm long and from 2.5 to 7.0 mm broad, the largest plants so far seen being from Port St. Johns. Larger plants, 1 cm or more in length, were growing with the dwarf plants at Brandfontein and at East London in 1965, but they differed from typical dwarf plants in a number of respects. The thalli were irregular in form, greenish in colour and had completely smooth, sterile margins with no sign of either monospores or serrations. In other words, they looked like very small, typical *P. capensis* plants. Some of the largest dwarf plants in the East London material showed evidence of the loss of the marginal serrations which appeared to be eroding away (Fig. 4. C.).

DISCUSSION

The most striking feature to be revealed as a result of detailed study of the full-sized parenchymatous phase of *P. capensis* is the wide range of variation in morphology, cell structure and arrangement of reproductive bodies which it exhibits. Previous workers (Agardh 1883, Issac 1957) have recognized that thallus form alone is of little value as a taxonomic character in this case. Of greater interest is the range of variation in cell structure and, more particularly, in spore arrangement which affects characters commonly used in the delimitation of species in *Porphyra*.

It has been shown that variations in vegetative cell form and structure are mainly expressions of developmental change, the pattern of development probably being influenced to some extent by environmental conditions. Furthermore, none of the three variations in spore arrangement which have been described is consistently associated with any other feature, either morphological or structural and there is at present no explanation for the occurrence of these variations. It is of interest to note in this connection that variations in spore development and arrangement described by Hus (1902) for *P. perforata* J. Ag. and *P. perforata* f. *lanceolata* Setchell and Hus (*P. lanceolata* (Setchell and Hus) G. M. Smith 1944) bear a striking resemblance to those found in *P. capensis*. Hus separates *P. perforata* f. *lanceolata* from *P. perforata* mainly on the grounds that the form is dioecious while the species is monoecious with irregular alternating patches of carpospores and spermatia. However, in describing f. *lanceolata* Hus states (p. 209) "occasionally forked fronds are met with and in such cases it is not unusual to find one fork bearing antheridia, while the other is strictly sporocarpic. These subdioecious fronds form a connecting link between the form and the species proper".

Whatever the explanation of these phenomena may be, the author is of the opinion that the taxonomic significance of spore arrangement must be regarded as suspect until the whole basis of reproduction in *Porphyra* is more clearly

understood and therefore agrees with Isaac (1957) in recognising a single species of intertidal South African *Porphyra*. Isaac gives the name as *P. capensis* Kütz. emend Agardh, but in the author's opinion, there is some doubt as to whether Agardh (1883) was dealing with a wide enough range of forms to make an amendment to the original name of *P. capensis* Kütz. necessary.

The general morphology, structure and intertidal position of the dwarf plants described strongly suggest that they represent a form of *P. capensis*. While they would appear to be similar in morphology and method of spore production to the dwarf plants of *P. tenera* as described by Tseng and Chang (1955), it is not possible at present to say what part dwarf plants may play in the life cycle of *P. capensis*. The known distribution range of dwarf plants is confined to the south and east coasts of South Africa, where the *P. capensis* association is poorly developed or absent. In this region the range of average annual water temperature is about 17°C to 22°C as compared with 13·0°C to 15·5°C for the west coast (Isaac 1957). There are therefore, indications of a relationship between water temperature and thallus development and behaviour reminiscent of that reported for *P. tenera* by Tseng and Chang. The possibility that dwarf plants of *P. capensis* may, like those of *P. tenera*, continue growth after spore production ceases and develop into full-sized plants, is indicated by the occurrence at Brandfontein and East London of thalli intermediate in type between dwarf and typical full-sized plants.

The dwarf plants of *P. umbilicalis* and *P. purpurea* as described by Conway (1964, 1966) would appear, at first sight, to be rather different in behaviour from those of *P. capensis*. Conway's figures for *P. umbilicalis* (1964 Fig. 15 and Plate II Fig. 11) show the release of spores from thalli which are at a very early stage of development, in one case consisting of only three cells. Dwarf thalli of *P. purpurea* apparently behave in a similar manner. However, since the dwarf plants of both these species are known only from cultures, any comparison of their behaviour with that of the South African material in the field is liable to be of doubtful significance.

The present study of *P. capensis* indicates that environmental factors may profoundly influence the morphology, anatomy and reproduction of this species. Conway (1966), in drawing attention to the highly flexible behaviour of the spores of *P. umbilicalis*, *P. purpurea* and *P. miniata*, has postulated that the mode of germination of both carpospores and conchospores is largely governed by environmental conditions. It therefore seems clear that one of the most urgent needs in any further study of *Porphyra* is for culture work under controlled conditions, so that the exact rôle of environmental factors in the biology of this genus may be assessed. Iwasaki (1961) and Dring (1967) have already

demonstrated the value of such work in respect of the *conchocelis*-phase. Attention might well now be focussed on culture techniques for the parenchymatous phase.

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